Energy density and variability in abundance of pigeon guillemot prey: support for the quality–variability trade-off hypothesis

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Summary

1. The quality–variability trade-off hypothesis predicts that (i) energy density (kJ g^{-1}) and spatial–temporal variability in abundance are positively correlated in nearshore marine fishes; and (ii) prey selection by a nearshore piscivore, the pigeon guillemot (*Cepphus columba* Pallas), is negatively affected by variability in abundance.

2. We tested these predictions with data from a 4-year study that measured fish abundance with beach seines and pigeon guillemot prey utilization with visual identification of chick meals.

3. The first prediction was supported. Pearson's correlation showed that fishes with higher energy density were more variable on seasonal ($r = 0.71$) and annual ($r = 0.66$) time scales. Higher energy density fishes were also more abundant overall ($r = 0.85$) and more patchy at a scale of 10s of km ($r = 0.77$).

4. Prey utilization by pigeon guillemots was strongly non-random. Relative preference, defined as the difference between log-ratio transformed proportions of individual prey taxa in chick diets and beach seine catches, was significantly different from zero for seven of the eight main prey categories.

5. The second prediction was also supported. We used principal component analysis (PCA) to summarize variability in correlated prey characteristics (energy density, availability and variability in abundance). Two PCA scores explained 32% of observed variability in pigeon guillemot prey utilization. Seasonal variability in abundance was negatively weighted by these PCA scores, providing evidence of risk-averse selection. Prey availability, energy density and km-scale variability in abundance were positively weighted.

6. Trophic interactions are known to create variability in resource distribution in other systems. We propose that links between resource quality and the strength of trophic interactions may produce resource quality–variability trade-offs.

Key-words: foraging, patchiness, resource heterogeneity, resource quality, risk sensitivity.

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Introduction

Risk-sensitive foraging behaviour occurs when animals make decisions in response to variability in resource distribution (Kacelnik & Bateson 1996). While risk sensitivity has been studied typically at the scale of individual foraging decisions, the sensitivity of animals to variability in foraging situations raises larger ecological questions that have received little attention. Several studies have demonstrated the importance of trade-offs between the mean values of correlated resource characteristics such as quality and quantity (Wright *et al*. 1998; Cruz-Riviera & Hay 2000), but the existence of risk sensitivity also raises the possibility that trade-offs between the mean and variance of different resource characteristics may be an important aspect of foraging ecology. If animals were sensitive to such covariation, then understanding the mechanisms producing covariation between the mean and variance of

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different characteristics would be an important goal in foraging ecology. Here we use the suite of prey available to breeding pigeon guillemots (*Cepphus columba* Pallas) as a model system for studying covariation in the mean and variance of different resource characteristics. Pigeon guillemots are nearshore-foraging seabirds of the auk family (Alcidae) that forage on both dispersed demersal fishes and aggregated pelagic fishes. Pelagic fishes such as sandeels (Ammodytidae) and herring (Clupeidae) typically have higher lipid levels than demersal fishes, and as a result are higher in energy density (kJ g^{-1}; Van Pelt *et al.* 1997; Anthony, Roby & Turco 2000). This difference in energy density is important to breeding pigeon guillemots as chick diets rich in pelagic prey increase energy provisioning rates, chick growth rates and reproductive success (Kuletz 1983; Golet *et al.* 2000; Litzow *et al.* 2002). In spite of the benefits of pelagic prey, pigeon guillemots and closely related black guillemots (*C. grylle*) have often been observed provisioning chicks with demersal prey in situations where pelagic prey are apparently abundantly available (Cairns 1987; Golet *et al.* 2000; Litzow *et al.* 2000). Kuletz (1983) and Cairns (1987) proposed as a solution to this paradox the hypothesis that low variability in demersal prey abundance offered an advantage that offset the advantage of higher energy density in pelagic prey. This hypothesis, which we refer to as the 'quality–variability trade-off' (QVT) hypothesis, holds that energy density is positively correlated with variability in abundance in nearshore fishes, and that *Cepphus* guillemots are adapted to the low energy density–low variability end of this spectrum. While demersal fishes are known to be less variable in abundance than pelagic fishes (Litzow *et al.* 2004), other key predictions of the QVT hypothesis have never been tested.

Our goals in this study were to test two predictions of the QVT hypothesis: (i) quality (i.e. mean energy density) and variability in abundance are positively correlated

within the suite of fishes available to pigeon guillemots; and (ii) pigeon guillemots are risk-averse, such that prey selection is negatively affected by variability in prey abundance. We used data collected in Kachemak Bay, Alaska during 1996–99 to test these predictions. Variability in prey abundance was measured with beach seines, prey utilization was measured with visual identification of pigeon guillemot chick meals and prey energy density was estimated from the literature. Finally, although the QVT hypothesis does not make explicit predictions about prey abundance, pelagic prey achieve mean levels of abundance one to two orders of magnitude greater than demersal prey in pigeon guillemot foraging habitat (Abookire, Piatt & Robards 2000). We therefore also tested the prediction that energy density and mean abundance are positively correlated in nearshore fishes.

Methods

DATA COLLECTION

We measured mean fish abundance and variability in abundance with beach seine catch per unit effort (CPUE; fish set^{-1}) in Kachemak Bay, Alaska (59°N, 151°W) from 1996 to 1999. Kachemak Bay is divided by Homer Spit into two oceanographically distinct sections (Fig. 1). The Inner Bay is dominated by river input and is warmer, less saline and more stratified than the Outer Bay, which receives oceanic input from the nearby Gulf of Alaska (Abookire *et al.* 2000).

Two lines of evidence suggest that beach seines measure prey availability accurately for pigeon guillemots. First, radio telemetry has shown that pigeon guillemots in Kachemak Bay forage mainly in the shallow (≤ 5 m) nearshore waters that beach seines sample (unpublished data). Secondly, seine catches are correlated with many pigeon guillemot breeding parameters, including
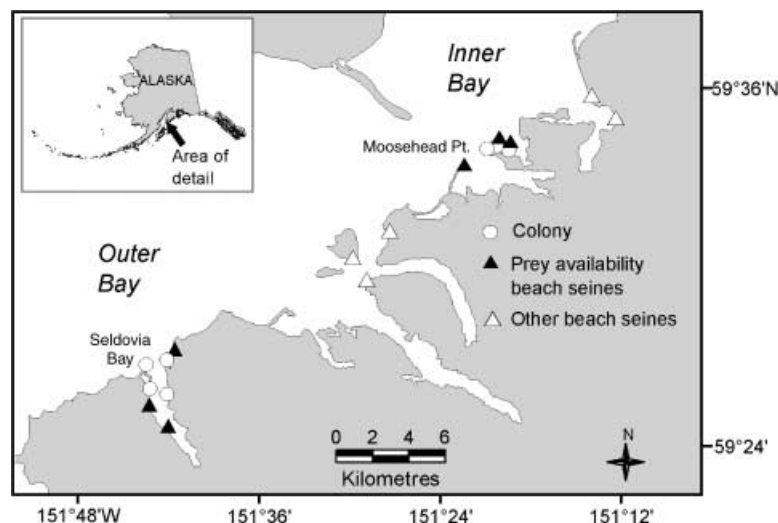
Fig. 1. Pigeon guillemot study colonies and beach seine stations in Kachemak Bay, Alaska. All beach seine stations were used in comparisons of prey energy density and variability in abundance. 'Prey availability beach seines' indicates those sites that were used to calculate prey availability for study colonies.

Table 1. Fish taxa with CPUE > 1 fish set^{-1} in beach seines in Kachemak Bay, Alaska. Source column refers to energy density data

Common name	Scientific name	Family	Primary habitat	Energy density (kJ g^{-1})	Source[a]
Capelin	*Mallotus villosus*	Osmeridae	Pelagic	4·45	1
Great sculpin	*Myoxocephalus polyacanthocephalus*	Cottidae	Demersal	3·31	1
Lingcod	*Ophiodon elongatus*	Hexagrammidae	Demersal	3·98	1
Pacific cod	*Gadus macrocephalus*	Gadidae	Demersal	3·45	1
Pacific herring	*Clupea pallasi*	Clupeidae	Pelagic	5·84	1
Pacific sand lance	*Ammodytes hexapterus*	Ammodytidae	Pelagic	5·40	1
Rock sole	*Lepidopsetta bilineatus*	Pleuronectidae	Demersal	3·36	1
Slender eelblenny, snake prickleback	*Lumpenus fabricii, L. sagitta*	Stichaeidae	Demersal	4·73	1
Whitespotted greenling	*Hexagrammos stelleri*	Hexagrammidae	Demersal	3·45	2

[a]1 = Anthony *et al*. (2000), 2 = Van Pelt *et al*. (1997).

diet composition; adult foraging effort; chick growth rate, survival rate and age at fledging; and reproductive success (Litzow *et al*. 2000, 2002; Litzow & Piatt 2003). We fished with a 44-m-long net every 2 weeks during June, July and August at 11 stations (*n* = 231 sets; methods in Litzow *et al*. 2000). Stations were separated by 1·5–16 km over 44 km of shoreline (straight line distance). Fish were identified to species, except for snake pricklebacks (*Lumpenus sagitta*) and slender eelblennys (*L. fabricii*), which could not be distinguished reliably in the field (taxonomic authorities for all fishes in Mecklenburg, Mecklenburg & Thorsteinson 2002). We were only interested in studying fishes that were common enough to be important prey for guillemots, and fishes that were caught often enough in beach seines to generate accurate abundance estimates. We therefore limited our analysis to taxa with CPUE ≥ 1 fish set^{-1}. We also excluded salmonids (Salmonidae) and saffron cod (*Eleginus gracilis*) from analysis because these taxa were mainly too large to be eaten by guillemots. Wet mass energy density was estimated by averaging published values (Table 1; Van Pelt *et al*. 1997; Anthony *et al*. 2000). Energy density data were selected to match size classes of guillemot chick meals (Litzow *et al*. 2000) and, when possible, the seasonal timing of chick rearing.

We used a data set of guillemot chick meals that were identified visually in Kachemak Bay during 1996–99 (Litzow *et al*. 2000) to examine the effects of variability in prey abundance on prey selection by guillemots. Meals were identified from anchored boats (using binoculars) or from hides (using telescopes), and were classified to the lowest possible taxonomic level. The majority of prey items (82%) were in eight classifications which were well sampled by beach seines: capelin (*Mallotus villosus*), flatfish (Pleuronectidae), gadids (Gadidae), greenlings (Hexagrammidae), Pacific herring (*Clupea pallasi*), Pacific sand lance (*Ammodytes hexapterus*), pricklebacks (*Lumpenus* spp.) and sculpins (Cottidae). The remaining 18% of prey items were in groups that were not well sampled by seines. These were mainly crescent gunnels (*Pholis laeta*) and hermit crabs (*Pagurus* spp.).

DATA ANALYSIS

We calculated variability in fish abundance on two temporal scales and two spatial scales. Interannual variability was calculated as coefficient of variation (CV) in CPUE among study years at each seine station. Seasonal variability was calculated as CV among seines set twice per month at a given station in a given year. Meso-scale (10s of km) variability was calculated as CV between the Inner and Outer Bays in each sampling period, and microscale (1s of km) variability was calculated as CV among stations within each area during each sampling period. We present seasonal and spatial CV values as grand means of annual means, and interannual CV as the mean of station values.

Analysis of prey selection was complicated by a lack of independence in response variables, as the proportion of different prey taxa in diets sums to 1. We therefore used the log-ratio transformation $y_i = \ln(x_i/x_j)$, where $x_1 \dots x_7$ represent the proportion of seven of the prey categories in the diet at a nest and x_j = the proportion of the eighth group ($i \neq j$). This transformation renders y_i linearly independently of each other (Aitchison 1986; Aebischer, Robertson & Kenward 1993), allowing us to use the proportion of individual prey groups at individual nests as our sample unit. Utilization of each of the eight prey categories at each nest (y_u) was calculated as the average of y_i calculated with each of the seven possible values of x_j, and prey groups absent from the diet at a particular nest were assigned a value of 0·01% of total diet (Aebischer *et al*. 1993). Prey availability (y_a) was measured with data from beach seines set within 3 km and 10 days of all-day watches of a given nest, and was defined with the log-ratio transformation of $\log_{10}(CPUE + 1)$ in the same manner as was used for prey utilization data. Relative preference (d) for each group was defined as $d = y_u - y_a$ (Aebischer *et al*. 1993). Thus values of $d > 0$ indicate groups that were consumed more than would be expected from their abundance, and values < 0 indicate groups that were consumed less than would be expected from their abundance. The null hypothesis of no difference between proportional use

and availability of prey groups was tested by averaging values of d among nests for each prey group, and calculating a t statistic as the ratio of mean to standard error of d, with d.f. = $n - 1$ (Aebischer *et al.* 1993).

We tested for risk-averse prey selection by comparing variability in abundance of various fish taxa with utilization by pigeon guillemots (y_u). We overcame multicollinearity in explanatory variables by summarizing variability in seasonal CV in abundance, km-scale CV in abundance, energy density and availability (y_a) with principal component analysis (PCA) and used the four resulting PCA scores as our explanatory variables. Meso-scale (10s of km) CV was excluded from this analysis because pigeon guillemots forage typically < 10 km from the nest, and interannual CV in abundance was excluded because most study nests were active only for a single year.

While visual methods allowed accurate identification of a large number of prey items the method provides low precision, as items could be identified typically only to the level of genus or family. For some groups (herring, sand lance, *Lumpenus* pricklebacks, capelin) visual categories matched categories in seine data. However, for other visual categories (sculpins, flatfish, greenlings, gadids), we could not distinguish visually among different prey species within a given family. In order to compare guillemot prey utilization with prey availability we therefore pooled seine data into the same classifications used in diet data. Energy density values for the visual categories were calculated by averaging values for every member of the group for which data were available (Van Pelt *et al.* 1997; Anthony *et al.* 2000). Energy density is relatively constant within families of demersal fishes (Anthony *et al.* 2000; Iverson, Frost & Lang 2002) and as a result, CV in energy density within visual categories was low (8–18%), suggesting that these averaged energy density values were representative for every member of a visual category. Taxa that were not well sampled by seines (CPUE < 1) were excluded from prey selection analysis.

Nests were included in prey selection analysis if at least 10 meals were identified (n = 36 nests, 877 meals, 233 prey group–nest combinations). These nests were from two areas of Kachemak Bay (Moosehead Pt and Seldovia Bay, Fig. 1), where radio telemetry showed a good spatial match between seine stations and guillemot foraging areas (unpublished data). Each nest was watched one to three times per year, and prey availability for each nest was therefore calculated from three to nine seine sets (i.e. three stations sampled one to three times each). To avoid pseudoreplication, we selected randomly a single prey group from each nest for inclusion in regression analysis of prey selection. Seasonal and km-scale CV for prey selection analysis were calculated for each nesting area in each year.

Results

We caught 232 224 fish. Nine taxa had a CPUE ≥ 1 fish set^{-1}, and these taxa made up 97% of the catch. Three of the nine taxa utilize primarily pelagic habitat and six are primarily demersal (Table 1). Average energy density was 40% greater for pelagic taxa (t_7 = 3·55, P = 0·01). Pelagic taxa also had higher mean abundance (log CPUE; t_7 = 3·17, P = 0·02) and higher interannual CV in abundance (t_7 = 3·32, P = 0·01).

Energy density had a significant overall effect on the four measures of variability in abundance as well as mean abundance (MANCOVA, Wilks's $\lambda_{5,3}$ = 0·02, P = 0·01). Univariate analysis showed that seasonal and mesoscale CV in abundance both increased with energy density (Fig. 1; Pearson's correlation, r ≥ 0·71, P ≤ 0·03), and there was a marginally non-significant positive relationship between energy density and interannual CV (r = 0·66, P = 0·053). We could not reject the null hypothesis of no relationship between energy density and km-scale CV in abundance (r = 0·55, P = 0·12). Log CPUE and energy density were correlated, so the correlations that we observed between CV in abundance and energy density could be an artefact of uncorrected heteroscedasticity in CPUE. We tested for this possibility by comparing log CPUE and CV in abundance for the nine taxa individually, using seine sites during individual years as our sample unit. One-tailed Pearson's correlations failed to find any positive correlations (P > 0·10). We could reject an alternate hypothesis of r = 0·66 (equal to the weakest significant correlation in our study) with power $(1 - \beta)$ = 0·52 for capelin and > 0·99 for other taxa.

Prey utilization was strongly non-random; proportional use and availability were significantly different for seven of the eight prey groups (Table 2). Backward stepwise regression (P to remain = 0·20) identified PCA2 and PCA4 as having significant effects on utilization (R^2 = 0·32, $F_{2,33}$ = 7·94, P = 0·002, Table 3). PCA1 (P = 0·29) and PCA3 (P = 0·61) were dropped from the model. PCA4 negatively weighted seasonal CV in

Table 2. Relative preference (d) by pigeon guillemots for eight prey groups. Preference is difference between log-ratio transformed utilization and log-ratio transformed availability, and is averaged among every study nest for which a particular group was available as determined by beach seines. Negative preference values indicate groups that were consumed less than would be predicted by their availability, positive values indicate groups that were consumed more than would be predicted by availability. Test statistics are for null hypothesis of no difference between proportional use and availability

| Group	Preference (d; mean ± SE)	t	d.f.	P
Capelin	−2·62 ± 0·31	−8·33	2	0·01
Flatfish	−0·22 ± 0·57	−0·39	35	0·70
Gadids	−3·56 ± 0·27	−13·01	35	< 0·0001
Greenlings	−3·18 ± 0·24	−13·37	28	< 0·0001
Lumpenus spp.	4·21 ± 0·71	5·91	31	< 0·0001
Pacific herring	−1·69 ± 0·28	−6·12	24	< 0·0001
Pacific sand lance	2·59 ± 0·83	3·12	35	0·004
Sculpins	1·40 ± 0·65	2·17	35	0·04

Table 3. Effects of prey characteristics on log-ratio transformed utilization (y_u) by pigeon guillemots. Parameter coefficients and test statistics are results from backward stepwise regression. PCA2 and PCA4 together explained 32% of variability in utilization ($F_{2,33} = 7.94$, $P = 0.002$). Two other PCA scores were dropped from the model ($P > 0.2$). Note that PCA2 positively weights energy density and availability while PCA4 negatively weights seasonal CV and positively weights km-scale CV

Factor	PCA2	PCA4
Eigenvectors		
Availability (y_a)	0·75	0·16
Energy density (kJ g^{-1})	0·68	0·08
Seasonal CV in CPUE	0·14	−0·68
Km-scale CV in CPUE	−0·10	0·71
Parameter coefficient ± SE	1·57 ± 0·61	2·92 ± 1·07
Partial R^2	0·14	0·15
t	2·58	2·72
P	0·01	0·01

abundance and positively weighted km-scale CV, and its positive regression coefficient (Table 3) suggested that selection was negatively affected by seasonal variability and positively affected by km-scale variability. PCA2 positively weighted availability and energy density and also showed a positive regression coefficient (Table 3), suggesting that these variables positively affected prey selection.

Discussion

Resource selection is usually explained either in terms of the quality and abundance of potential food items (Stephens & Krebs 1986; Wright *et al.* 1998; Cruz-Riviera & Hay 2000) or by the amount of variability present in food quality or abundance (Kacelnik & Bateson 1996; Shafir 2000). However, our results confirm the predictions of the QVT hypothesis that resource quality and variability in abundance are correlated in this system (Fig. 2), and both characteristics affect selection by pigeon guillemots (Table 3). Furthermore, resource abundance was also correlated with quality and variability in abundance, and also affected selection. This intercorrelation of resource characteristics that are important in determining prey selection demonstrates the importance of simultaneously measuring resource variability, quality and quantity in studies of foraging ecology. The nine fish taxa that dominated seine catches in this study come from eight families (Table 1) that are extremely common in the nearshore waters of the boreal Pacific and Atlantic oceans (Hart 1973; Scott & Scott 1988), so the patterns that we observed are likely to be widely representative. Many seabirds, marine mammals and fishes feed on both demersal and pelagic prey (Livingston 1993; Tremblay & Cherel 2000). The quality–variability trade-offs that we observed may therefore affect the foraging ecology of many marine predators.
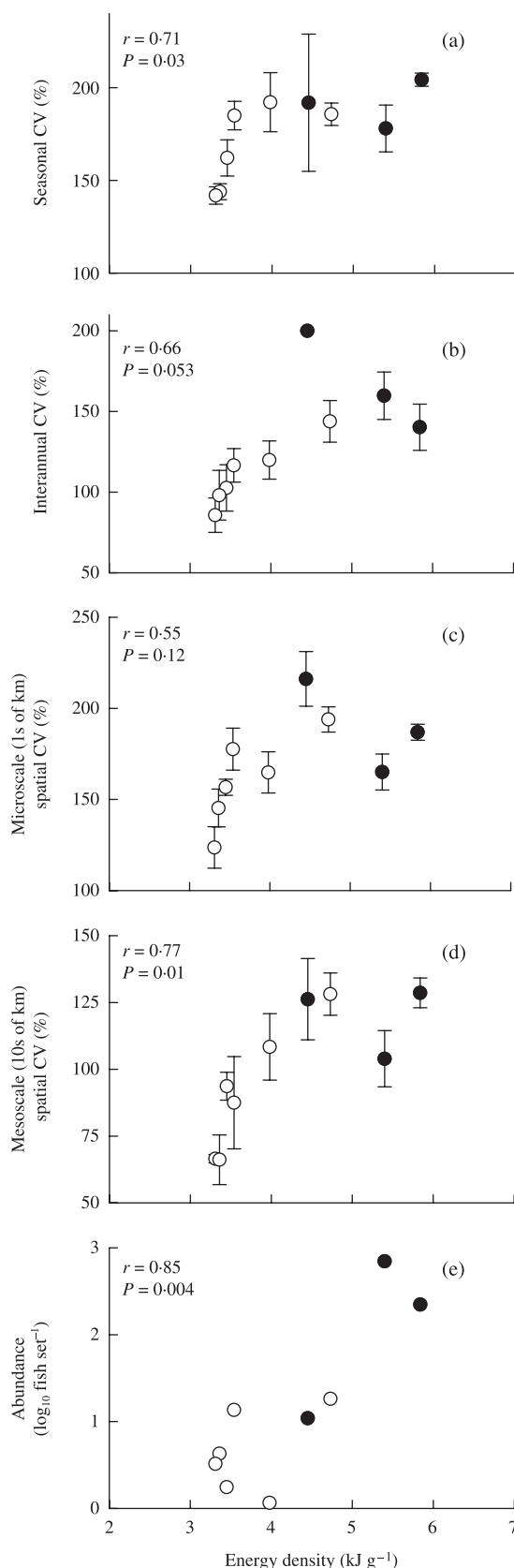
Fig. 2. Correlations between energy density of nearshore fishes and (a) seasonal CV, (b) interannual CV, (c) microscale CV, (d) mesoscale CV and (e) abundance. Open circles are demersal fishes, closed circles are pelagic fishes. Data are from beach seines set every 2 weeks at 11 stations during summer 1996–99 in Kachemak Bay, Alaska. Statistics are from Pearson's correlations, CV data are means ± SE.

IMPLICATIONS OF QUALITY–VARIABILITY
TRADE-OFFS

We could explain only a fraction (32%) of observed variability in guillemot prey utilization, which is typical given the complexity of natural foraging situations (Perry & Pianka 1997). Pigeon guillemot prey selection is likely affected by many factors not measured in this study, such as individual specialization (Drent 1965; Golet *et al*. 2000), easier capture of sedentary demersal fishes (George-Nascimento, Bustamente & Oyarzun 1985; Bowen *et al*. 2002) and competition for high-quality pelagic prey (Ballance, Pitman & Reilly 1997). Limitations of beach seining (e.g. limited sampling effort, imperfect overlap between foraging habitats and areas sampled, differences in species-specific catchability) also doubtless reduced our ability to explain variability in prey utilization.

PCA2 and PCA4 both positively affected selection by pigeon guillemots. The negative weighting of seasonal variability by one score, and the positive weightings of energy density and mean availability by another, suggest that guillemots seek to minimize temporal variability in prey abundance while maximizing prey quality and mean availability. The value of high prey energy density and availability has been demonstrated previously for a variety of seabirds (Piatt 1990; Brekke & Gabrielsen 1994; Ballance *et al*. 1997) and for pigeon guillemots in particular (Golet *et al*. 2000; Litzow *et al*. 2002). High variability in food abundance has long been viewed as an important factor in the evolution of seabird life histories (Ashmole 1971), and pigeon guillemots may be particularly sensitive to variable prey abundance. *Cepphus* guillemot parents maintain higher meal delivery rates than other auks, giving them the ability to raise two chicks to adult mass in the nest, which is unique in the family (Sealy 1973). The QVT hypothesis proposes that the ability to maintain high delivery rates is dependent on the low temporal variability of demersal prey abundance (Cairns 1987). This view agrees with the theoretical expectation that animals exploiting highly variable prey will experience stochastic periods of extremely low prey availability (Sutherland & Moss 1984). On interannual time scales, pigeon guillemots buffer against the high variability of pelagic prey with prey switching and flexible time–activity allocation (Litzow *et al*. 2002; Litzow & Piatt 2003). Although prey switching also occurs at the seasonal scale (Litzow *et al*. 2000), aversion to variability at this scale presumably reflects either high costs of buffering or limited ability to buffer at shorter time scales.

Spatial patchiness has been identified as a mechanism that allows differences in competitive ability, foraging efficiency and travel ability to structure communities of pelagic-feeding seabirds (Piatt 1990; Ballance *et al*. 1997). Our observation of a positive effect on prey selection by a PCA score that positively weights km-scale variability in abundance (Table 3) suggests that spatial variability

may provide similar advantages of resources partitioning among conspecific benthic-foraging seabirds. Prey exhibiting high spatial variability might also be advantageous to foraging guillemots simply because spatial clumping in resources may increase rates of resource gain (Stephens & Krebs 1986).

CAUSES OF QUALITY–VARIABILITY
TRADE-OFFS

Why is the energy density of fishes correlated with variability in abundance? Both bottom-up and top-down trophic interactions are known to produce resource heterogeneity in terrestrial systems, as variability in the abundance of abiotic resources may propagate variability up trophic webs (Clutton-Brock 1974; Jarman 1974; Wilby & Shachak 2000) or heterogeneous foraging intensity may create variability in lower trophic levels (Wiens 1976; Bohan *et al*. 2000; Wilby & Shachak 2000; Winder *et al*. 2001). Both bottom-up and top-down processes may also drive variability in marine fish abundance. Dynamic physical features of the water column produce heterogeneous patterns of energy and nutrient availability that result in patchy primary production (Valiela 1995). Active aggregation of grazing zooplankton at phytoplankton patches is in turn an important driver of patchiness in the distribution of prey of small pelagic fishes (Folt & Burns 1999). Conversely, top-down drivers of variable fish abundance have been inferred from patterns of seabird colony distribution and inverse correlations of colony size and reproductive success (Furness & Birkhead 1984), as well as through direct observation of prey depletion around colonies (Birt *et al*. 1987). Top-down mechanisms may also result in spatial heterogeneity if predator avoidance depresses fish abundance around colonies (Lewis *et al*. 2001).

The physiological quality of food is intimately connected with both bottom-up and top-down processes, suggesting a mechanism that may link food quality (energy density or nutrient content) with variability in food abundance. Bottom-up controls on food quality for terrestrial herbivores are well known. For example, rapidly growing grasses that exploit high-rainfall habitats are higher-quality food for antelopes than slow-growing shrubs that exploit low-rainfall habitats (Jarman 1974). Heterogeneity in rainfall also makes grasses spatially and temporally more variable in abundance than shrubs (Jarman 1974), so bottom-up processes link food quality and heterogeneity in this system. Covariation of food quality and variability in abundance in marine systems may also be driven by bottom-up processes. For example, crustaceans fed upon by pelagic fishes contain more energy than benthic crustaceans, perhaps because they have evolved lipid stores in response to the greater variability and unpredictability of pelagic habitats (Norrbin & Båmstedt 1984). Similarly, pelagic fishes are widely ranging predators that exploit localized areas of high productivity

(Valiela 1995), which probably explains both the high abundance and variability in abundance of pelagic species, as well as their ability to maintain energetically expensive lipid reserves. Links between food quality and patterns of availability due to top-down processes arise when higher-quality, preferred foods experience more consumer pressure (and resulting heterogeneity) than lower-quality foods (Wiens 1976; Wilby & Shachak 2000). Higher-quality pelagic fishes are preyed upon by seabirds more often than demersal fishes (Furness 1996), suggesting a possible top-down link between quality and variable abundance in our study system.

Much research has demonstrated that variability in food abundance and variability in food quality have important consequences for consumers. Less work has focused on mechanisms that link food quality to variability in abundance. If bottom-up and top-down sources of variability in abundance also have implications for quality, then the covariation that we observed between resource quality and variability in abundance may exist in many foraging situations. If so, quality–variability covariation will provide a useful conceptual framework for synthesizing current knowledge about the roles that food quality and variability in abundance play in foraging ecology.

Acknowledgements

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